A Neuronal Correlate of Octave Similarity and Discrimination in the Auditory Midbrain of Gerbils

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Introduction

A common feature of acoustic signals, especially in human and animal communication, is amplitude modulation. In addition to the frequency analysis of the cochlea the periodicity of signal envelopes is processed in the brainstem and results in periodicity tuned neurons and a periodotopic map in the inferior colliculus (IC).

Models employing coincidence analysis (i.e. [4], [5]) are a reasonable approach to explain periodicity tuning. The autocorrelation $AKF(\Delta\tau) = \int f(t) * f(t-\Delta\tau)\, dt$ has high values if the periodicity of the signal f(t) fits to the delay $\Delta\tau$, but also if the delay is a multiple of the signal periodicity (octaves and higher harmonics of BMF, comb-type). This is in contrast to the commonly observed band pass tuning in the IC [7]. To understand the preponderance of band pass tuned neurons we investigated the response of neurons in the IC of awake gerbils to sounds with periodic envelopes. All investigated neurons had typical tuning curves for pure tones and well defined characteristic frequencies. Stimulated with sinusoidal amplitude modulated tones (SAM) many showed tuning to the units best modulation frequency (BMF). We examined the time course of periodicity tuning and the possible role of temporal inhibition.

Method

Single unit recordings were obtained from awake gerbils *(Meriones unguiculatus)* using Tungsten electrodes (5 MΩ). The system was calibrated using an electrostatic Microphone and a digital signal processor for stimuli generation. The stimuli were converted and presented by a loudspeaker with high temporal fidelity (Manger) placed 20 cm in front of the animal. The recording was controlled by a spikes sorting software, which collected the neuronal activity.

Tuning curves were examined with pure tones of varying frequency and levels. The best frequency (about 20dB above threshold) was modulated with pure tones in a way to obtain a full first cycle (2ms $\cos^2$-ramp added to reduce onset clicks). By applying different SAM-Stimuli the modulation transfer function (MTF) was measured in small evaluation windows (~20 ms) with different onsets to examine the time course of the MTF. The duration of these windows were chosen as integer multiples of the modulation period to minimize distortions due to phase coupling. Iontophoretic studies used four barrel piggy back electrodes. The recording and the balancing barrel were filled with 3M NaCl solution. Two barrels were filled with GABA and glycine receptor antagonists, 10mM bicuculline methiodide (bic, pH 3, 15nA retention, 20nA ejection current) and 10nM strychnine sulfate (str, pH 3, 15nA retention, 60nA ejection current). The application of the drugs started 2 minutes before recording.

Results

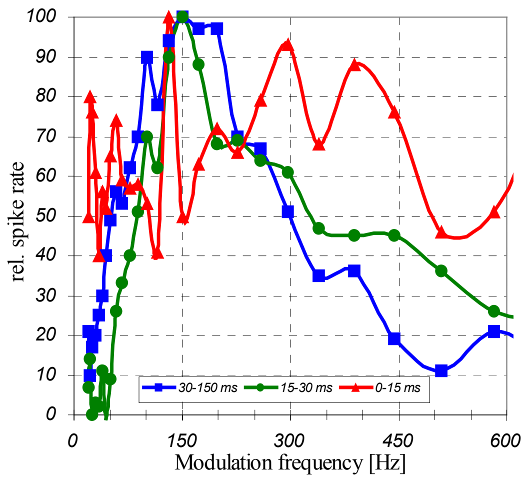

Figure 1: MTFs measured at different time intervals. At Onset (red) the BMF, its octave and 3rd harmonic causes a neuronal response, later (green and blue) only the BMF remains.

In small time intervals shortly after the onset of SAM, responses to the octave of the BMF and even higher harmonics occur (0-15 ms, Fig. 1). In the late time window (green: 15-30 ms, blue: 30-150 ms) the harmonic reactions are suppressed and the unit shows band pass tuning to a particular BMF (150 Hz). 45% of the BMF-tuned neurons (n=70) showed comb-type MTFs (Fig. 2) at stimulus onset. As a result such neurons indicate the similarity of octaves and also higher harmonics.

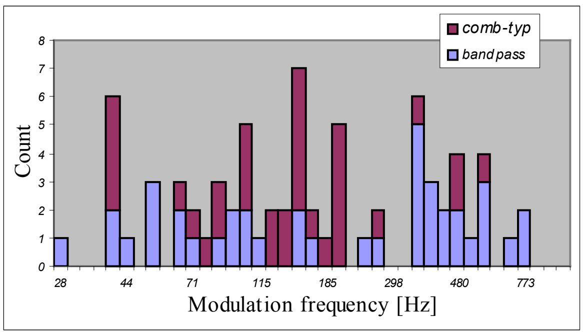

Figure 2: Distribution of BMFs observed in the ICC (n=70). Violet bars correspond to units with transient reactions to the octave or even higher harmonics of their BMF (n=33).

Interpolation of modulation frequencies at maximal reactions of one neuron by cubic splines generates a diagram of the time course of reactions (Fig. 3). As the evaluation time interval is shifted along the time axis suppression of the harmonics increases and harmonic reactions get non significant (orange). Up to 15 – 40 ms the response to 2*BMF (octave) is similar to the response to the BMF

(Fig. 4). Later it nearly vanishes, leaving only one peak at BMF. A possible explanation for suppression of comb-type reactions would be phase coupled inhibition.

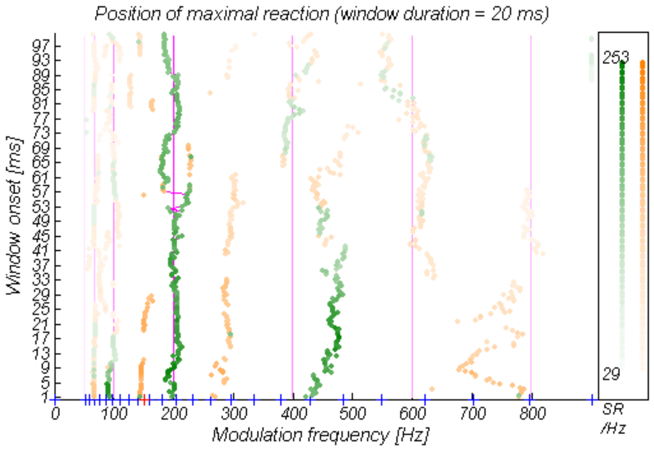

Figure 3: Time course of periodicity tuning of one neuron. Modulation frequency and spike rate (colour code) of maximal reactions in MTFs calculated for different evaluation windows are marked. Vertical lines indicates the units BMF and multiples of the BMF.

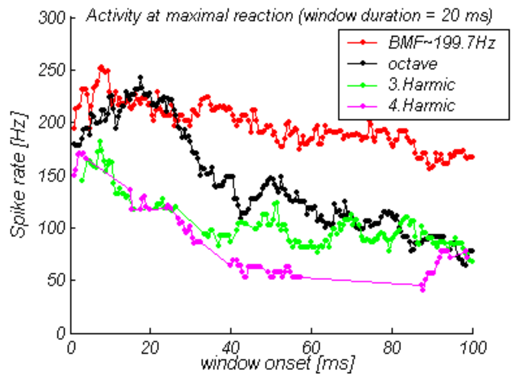

Figure 4: Suppression of reaction to harmonics (as shown in Fig. 3).

A MTF for one neuron from a late time interval with and without blocking of inhibition is shown in Figure 5. When inhibitory inputs are blocked the unit reacts much stronger to its BMF and also to harmonics of BMF. The phase angle is increased by blocking inhibition (Fig. 6) supporting the assumption that inhibition is strongest immediately after phase coupled responses. Further evidence for synchronized inhibition with a duration appropriate for suppression of the higher harmonics was found in the on-response in units with low BMFs. The suppression of the reactions to multiples of the BMF seems to be a second filter mechanism for periodicity coding in addition to the coincidence of delayed and undelayed responses to modulation cycles. A possible mechanism is an inhibition which is triggered by the envelope of the signal [2]. This filter mechanism depresses reactions of IC neurons to periodic acoustic signals if the period is twice or more the neurons BMF. The duration of the inhibition τ_I must fulfill the relation: $\tau_{BMF}/2 < \tau_I < \tau_{BMF}$. A possible source of this inhibition is the ventral nucleus of the lateral lemniscus. It receives precisely timed input by giant synapses form the octopus cells [1], it provides an inhibitory projection to the IC [3] and has a periodotopic organization [6]. We conclude that periodicity coding is based on a superposition of high-pass and low-pass filters, a sharply tuned comb-type filtering due to a correlation analysis (high-pass) and a filtering due to timed inhibition (low pass).

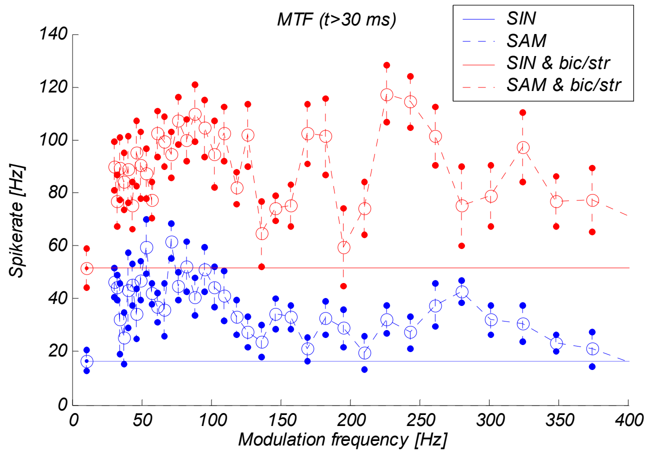

Figure 5: MTFs from one unit obtained with (red) and without application of inhibitory receptor antagonists (blue). Without inhibiton reactions to harmonics of BMF occur.

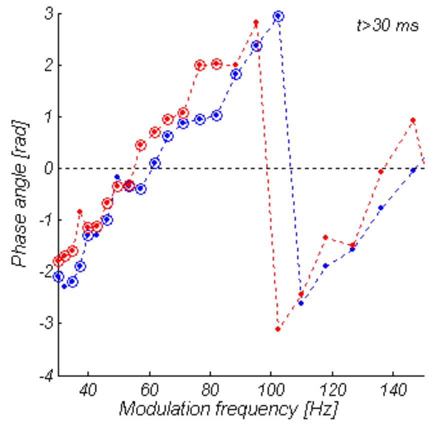

Figure 6: Phase angle of responses. Blocking inhibitory receptors (red) leads to delayed responses.

Literature:

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